Issued November 23, 1908.

U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF PLANT INDUSTRY—Circular No. 18.
B. T. GALLOWAY, Chief of Bureau.

REAPPEARANCE OF A PRIMITIVE CHARACTER IN COTTON HYBRIDS.

BY

O. F. COOK,

Bionomist, Bureau of Plant Industry.

59001—Cir. 18—08

WASHINGTON : GOVERNMENT PRINTING OFFICE : 1908

BUREAU OF PLANT INDUSTRY.

Physiologist and Pathologist, and Chief of Bureau, Beverly T. Galloway.
Physiologist and Pathologist, and Assistant Chief of Bureau, Albert F. Woods.
Laboratory of Plant Pathology, Erwin F. Smith, Pathologist in Charge.
Investigations of Diseases of Fruits, Merton B. Waite, Pathologist in Charge.
Laboratory of Forest Pathology, Haven Metcalf, Pathologist in Charge.
Cotton and Truck Diseases and Plant Disease Survey, William A. Orton, Pathologist in Charge.
Plant Life History Investigations, Walter T. Swingle, Physiologist in Charge.
Cotton Breeding Investigations, Archibald D. Shamel and Daniel N. Shoemaker, Physiologists in Charge.
Tobacco Investigations, Archibald D. Shamel, Wightman W. Garner, and Ernest H. Mathewson, in Charge.
Corn Investigations, Charles P. Hartley, Physiologist in Charge.
Alkali and Drought Resistant Plant Breeding Investigations, Thomas H. Kearney, Physiologist in Charge.
Soil Bacteriology and Water Purification Investigations, Karl F. Kellerman, Physiologist in Charge.
Bionomic Investigations of Tropical and Subtropical Plants, Orator F. Cook, Bionomist in Charge.
Drug and Poisonous Plant Investigations and Tea Culture Investigations, Rodney H. True, Physiologist in Charge.
Physical Laboratory, Lyman J. Briggs, Physicist in Charge.
Crop Technology and Fiber Plant Investigations, Nathan A. Cobb, Crop Technologist in Charge.
Taxonomic and Range Investigations, Frederick V. Coville, Botanist in Charge.
Farm Management Investigations, William J. Spillman, Agriculturist in Charge.
Grain Investigations, Mark Alfred Carleton, Cerealist in Charge.
Arlington Experimental Farm, Lee C. Corbett, Horticulturist in Charge.
Vegetable Testing Gardens, William W. Tracy, sr., Superintendent.
Sugar-Beet Investigations, Charles O. Townsend, Pathologist in Charge.
Western Agricultural Extension Investigations, Carl S. Scofield, Agriculturist in Charge.
Dry-Land Agriculture Investigations, E. Channing Chilcott, Agriculturist in Charge.
Pomological Collections, Gustavus B. Brackett, Pomologist in Charge.
Field Investigations in Pomology, William A. Taylor and G. Harold Powell, Pomologists in Charge.
Experimental Gardens and Grounds, Edward M. Byrnes, Superintendent.
Foreign Seed and Plant Introduction, David Fairchild, Agricultural Explorer in Charge.
Forage Crop Investigations, Charles V. Piper, Agrostologist in Charge.
Seed Laboratory, Edgar Brown, Botanist in Charge.
Grain Standardization, John D. Shanahan, Crop Technologist in Charge.
Subtropical Laboratory and Garden, Miami, Fla., Ernst A. Bessey, Pathologist in Charge.
Plant Introduction Garden, Chico, Cal., W. W. Tracy, jr., Assistant Botanist in Charge.
South Texas Garden, Brownsville, Tex., Edward C. Green, Pomologist in Charge.
Farmers' Cooperative Demonstration Work, Seaman A. Knapp, Special Agent in Charge.
Seed Distribution (Directed by Chief of Bureau), Lisle Morrison, Assistant in General Charge.

Editor, J. E. Rockwell.
Chief Clerk, James E. Jones.

REAPPEARANCE OF A PRIMITIVE CHARACTER IN COTTON HYBRIDS.

INTRODUCTION.

The facts considered in this brief report are incidental results of experiments undertaken for the purpose of acclimatizing in the United States weevil-resistant varieties of cotton from Central America and of hybridizing them with our United States varieties. The experiments have not yet been carried far enough to determine the agricultural value of these varieties in the United States, but they have already afforded several facts of scientific and practical interest.

It is demonstrated that hybrids may differ from both parents in showing undesirable primitive characters in the first generation and yet may be free from such characters in the second generation. An explanation of this strange behavior is found in the fact that the first generation of hybrids represents an intermediate stage in the process of conjugation begun by the original germ cells, while the second generation is formed after a complete conjugation has taken place.

Thus breeders have an additional reason for growing their hybrids for at least two generations. To reject first-generation hybrids because they appear unpromising is to judge them before the experiment of crossing is really complete. It is like throwing away young plants or animals because they do not have all the properties of adults. Instead of being accepted as evidence regarding the agricultural value of hybrids between two species or varieties the characters of the first generation may be merely temporary. Hybrids which do not yield a desired combination of parental characters in the first generation may still do so in the second generation.

PRIMITIVE CHARACTERS SHOWN IN REVERSION AND RECAPITULATION.

Any character which appears to have been attained far back in the developmental history of a species or variety may be described as a primitive character. The name is applied more especially to characters which have ceased to be regularly expressed, but come to light only in occasional individuals which are said to "take after" remote ancestors instead of resembling their immediate parents.

Facts showing the persistence of primitive characters in plants and animals are commonly recognized as constituting two distinct groups of phenomena, called reversion and recapitulation. The behavior of

our cotton hybrids seems to show that the relation between these phenomena is very intimate, and that one may pass into the other as a result of hybridization.

Reversion is the reappearance of a character which has been transmitted in latent form—that is, without being brought into expression in the parent generation or in a previous series of generations. Recapitulation may be described as the following over of the ancestral paths of descent in each generation. Studies of the embryology of the higher vertebrates have shown that many primitive features are brought into temporary expression in the course of development of each individual. Mammalian embryos still show gill clefts and rudiments of other ancestral features which have not served as adult characters for many geologic ages.

Reversion and recapitulation have no limits in years or in numbers of generations. They give us a vivid indication of the all-embracing, all-enduring power of transmission. Darwin has aptly associated the permanence of latent characters with the persistence of rudimentary organs:

> There is no more inherent improbability in each domestic pig, during a thousand generations, retaining the capacity and tendency to develop great tusks under fitting conditions, than in the young calf having retained for an indefinite number of generations rudimentary incisor teeth, which never protrude through the gums.[a]

In this, as in many other passages, Darwin recognizes a distinction which many subsequent writers have overlooked, perhaps because no definitely contrasted terms were used to define it. The distinction is between (1) the process of transmission which conveys to successive generations of organisms the "capacity and tendency" to reproduce and transmit the characters of their parents and ancestors, and (2) the process of expression, by which characters are actually "developed" or worked out in visible form. These two processes, transmission and expression, give us the facts commonly known as "heredity."

Recapitulation may be described as a temporary or partial expression of a primitive character, while reversion is the expression of a character which is usually transmitted in latent form without coming into expression at all. Recapitulation may never be visibly complete; many ancestral characters are not brought into expression, but the power of such characters to reappear shows that they continue to be transmitted. The "capacity and tendency" remain in the protoplasm, even when no visible tissues are formed. The many different reversions shown by members of the same stock indicate that all the ancestral characters are probably transmitted and con-

[a] Darwin, Charles. Variation of Animals and Plants under Domestication, chapter 13.

tinue to be capable of regaining expression if some unusual condition interferes with more normal courses of development. Hybridization and transfer to new conditions are the most familiar means of calling forth the latent characters.

The course of development followed by any individual plant or animal is chosen, as it were, from many ancestral alternatives. Though only the chosen characters are brought into expression, the process of transmission remains inclusive and impartial. Each generation is to be thought of as passing along to its successors a complete genealogical chart. Galton's law of regression shows that each generation tends to follow the routes used by the parents and other recent ancestors, but under normal conditions of descent there is a wide liberty of choice. Individual diversity is persistently shown, even when organisms of the same ancestry develop under the same conditions.

REAPPEARANCE OF GREEN FUZZ IN COTTON HYBRIDS.

Reversion is often reckoned as a rare and exceptional phenomenon, not to be understood from the standpoint of normal inheritance; but the fact is that many reversions are as definite and uniform as any other processes of descent. Thus there are no characters in which hybrids between the Kekchi cotton of Guatemala and the Sea-Island or Egyptian cottons are in better agreement than in the very large size of the seeds and in the dense coat of bluish green fuzz with which the seeds are covered underneath the long, white lint. These characters render the seeds of the hybrids abruptly different from those of the parent types.

The removal of the lint leaves the seeds of the Kekchi cotton covered with a dense white fuzz, while the seeds of the Sea-Island and Egyptian cottons are black and naked. Thus the green fuzz of the hybrid seed is not a blend or other combination of the parental characters, though it may be viewed as a compromise between the parental conditions if considered in relation to other facts of reversion and recapitulation. Examples of green fuzz are found in many different types of cotton, including those which are native in the Old World, and especially in wild or unimproved varieties. Thus it probably represents an ancestral condition from which both of the parental types have diverged. No wild cottons with white fuzz seem to be known, but most of the naked-seeded cottons have a small tuft of green or brown fuzz at the base of the seed. A Guatemalan cotton of the Sea-Island series has the lower half of the seed coated with green fuzz, the lint being confined to the upper half, which has no fuzz.[a]

[a] Cook, O. F. Weevil Resisting Adaptations of the Cotton Plant, Bulletin 88, Bureau of Plant Industry, U. S. Dept. of Agriculture, p. 32.

The reappearance of the green fuzz in these hybrids need not be considered as a turning back from the characters of the parent varieties, as the word reversion seems to imply. These hybrids do not follow either of the parental routes of development, but compromise on a primitive character which appears to represent common ancestral ground. A stage of development which is quickly passed by or entirely latent in the parent varieties remains as a definitely expressed character of the hybrids. Abortive seeds are often found with green fuzz, even when normally matured seeds in the same locks have white fuzz. Thus reversions can be viewed as conditions of arrested development—failures to pass beyond stages marked by primitive characters.

DIFFERENCES BETWEEN FIRST AND SECOND GENERATIONS.

The recall to expression of the ancestral green-fuzz character is not permanent. The next generation shows a wide diversity of combinations and intergradations between the characters of the parent types, but there is no such failure to attain the parental characters as in the first generation, though the green color sometimes remains in the second and even in the third generation. Why an ancestral character should so regularly appear in the first generation and almost as regularly disappear in the second is not easily understood until we remember that the second generation is the first that represents a completion of the conjugation begun by the original germ cells.[a]

The first generation is formed during the preliminary stages of conjugation, so that the temporary expression of an ancestral character in the first generation may not be essentially different from other phenomena of recapitulation in which temporary expression of characters takes place. Instead of an intermediate average between the divergent parental characters or the dominance of one over the other, the green fuzz may represent a third method of adjusting the parental differences, by compromising upon a common ancestral character.

If we think of the green fuzz as in the nature of a chemical combination of the parental characters, its failure to become "fixed" appears very mysterious; but when we associate it with the phenomena of reversion and recapitulation it is easy to understand that the disappearance of the green in the second generation accords with the very frequent result that the second generation of a hybrid differs from the first. An intermediate and nearly uniform first generation often produces an extremely diversified second generation.

The experiments of Mendel and his successors have made us familiar with the fact that parental characters which are suppressed

[a] Cook, O. F., and Swingle, W. T. Evolution of Cellular Structures. Bulletin 81, Bureau of Plant Industry, U. S. Dept. of Agriculture, 1905.

in the first generation commonly reappear in the second generation. The first generation of a Mendelian hybrid shows only one of a pair of contrasted parental characters (called the dominant character) but the other character (recessive) reappears in a part of the second generation. The behavior of the green-fuzz character may be described as a converse of typical cases of Mendelism, for a character very prominent in the first generation tends to disappear in the later generations. This is true even in crosses between the white-seeded Kekchi cotton and normally green-seeded Upland varieties, like the Truitt. Though the green-seeded character predominates in the first generation, it gradually disappears in the second and third generations. A similar departure from the Mendelian behavior is shown in a hybrid in which the smooth-seeded character appeared to be dominant in the first generation, while about two-thirds of the plants of the second generation have the seeds fuzzy in different degrees. In a few of them the fuzz is greenish, but none have the vivid green usually shown when the color appears in the first generation.

EXPRESSION OF CHARACTERS IN FIRST AND SECOND GENERATIONS.

Differences between the first and second generations of hybrids are the external evidence of the fact that the processes of reproduction followed by the higher plants and animals have two critical points or periods of adjustment of the internal relations which govern the expressions of the characters. One adjustment is made when conjugation begins by the union of the outer protoplasm and nuclei of the two germ cells. A second adjustment is made when conjugation is completed by the fusion of the chromatic material of the cells (mitapsis) before the formation of the germ cells which give rise to the second generation. The adjustments made when the conjugation of the germ cells begins are usually less profound than those accomplished when conjugation is completed.

The first adjustment has the single result of determining the expression of characters in the first generation—that in which the conjugation begins. The results of the second adjustment are not shown until the second generation, which is in reality the first generation to be formed after conjugation has been completed by mitapsis. The second generation often shows a very different series of adjustments, and often a widely varied series. Individual members of this generation frequently differ as much from each other as from the parental types.

If characters combined like other physical or chemical substances we might expect that like ingredients would produce like results, whereas hybrids of the same parentage may be endlessly diverse.

The facts of reversion and recapitulation enable us to look upon these diversities of hybrids as corresponding to the normal diversities of descent of the parental groups intensified by the recall to expression of ancestral peculiarities, such as the green fuzz of the cotton hybrids.

If the green-fuzz character behaved in a truly Mendelian manner half of the second generation would have green seeds. The theory of Mendelism holds that characters are transmitted as separate "units" and that the units which represent definitely contrasted parental characters pass into separate germ cells at the end of the first generation. Thus the germ cells formed by the green-seeded first generation would carry either the black-seeded Egyptian character or the white-seeded Kekchi character. Half of the germ cells would conjugate with others of their own kind and half would find mates of the opposite kind. The contrasted pairs would give rise to green-seeded plants, while the other half of the second generation would be equally divided between white seeds and black seeds.

The general disappearance of the green seeds in the second generation indicates that the germ cells which produce this generation do not have the same expression relations as those which produced the first generation, for there is not the same tendency to recall the green fuzz into expression. Development no longer halts at this earlier stage, but brings back the white fuzz and the smooth seeds of the parent types and many intermediate conditions. The parental characters are not only united with each other in varying combinations, but also in combination with occasional traces of the green fuzz or of brown fuzz, a character which also appears in primitive types of cotton. Traces of green or brown fuzz may even arrive without hybridization, as when the Kekchi cotton is being raised for the first time in the United States, or when our Upland varieties are grown in new localities. Exposure to new conditions disturbs the usual course of development and brings many latent diversities into expression, often the same diversities that are found among the hybrids.

Different crosses between the same stocks may show different degrees of expression of the green character. Sometimes it does not appear in the first generation and sometimes it lingers in a large proportion of the second generation. The strongest tendency to retain the green fuzz has been noticed in a hybrid which had the Jannovitch Egyptian cotton for the female parent and the Kekchi cotton for the male parent. In one planting of thirty second-generation individuals raised from a green-seeded plant of the first generation, twenty show at least a trace of green in the fuzz, five have the seeds nearly smooth, and five others have them densely covered with white fuzz. Among the twenty reckoned as having green seeds there are many gradations in the color as well as in the amount of fuzz on the seeds.

EXPRESSION OF CHARACTERS DETERMINED BY ADJUSTMENTS.

It is not necessary to suppose that the return of the parental characters in the second generation of the cotton hybrids is caused by a mere reversal or undoing of the internal adjustments which led to the formation of the green seeds, as the theory of Mendelism assumes. The probability is rather that the parental characters return because further and more complete adjustments have been reached. Even from the standpoint of Mendelism it has to be recognized for the first generation that the expression relations of the characters are determined by adjustment.

There is no reason to believe that either of the germ cells which have formed one of the green-seeded hybrids was adjusted to bring the green-seed character into expression. The green-seed character would have continued to remain in abeyance if either of the germ cells which give rise to a green-seeded hybrid had conjugated with a partner of its own kind. But after the conjugation began, the tendencies of expression were changed and the green-seeded character appeared.

Under the theory of Mendelism two different assumptions are used in attempting to explain the two changes of characters, away from the parents and then back again. It has to be considered that the characters of the first generation are determined, as stated, by a readjustment of the internal relations which govern the expression of the characters. But when the end of the generation is reached and new germ cells are to be formed Mendelism assumes that the expression relations of the new cells are determined in another and very different way, by the segregation of the "units" of the contrasted parental characters in distinct germ cells.

The assumptions of Mendelism, that the characters are represented by "units" and that these are segregated and are transmitted by different germ cells, become unnecessary as soon as we consider that the expression relations of germ cells may be determined by adjustment. The fact that the expression relations of germ cells are capable of being readjusted after conjugation should be considered as evidence that the relations they have before conjugation are also reached by adjustment rather than by exclusion. If characters are to be thought of as represented in the germ cells by definite particles or material "units" of any kind, it is more in accord with the facts to think of these particles as changing some positional, chemical, or other relation among themselves than as being separately transmitted in different germ cells.

Such facts as the reappearance of the green fuzz in the first generation of these cotton hybrids show that the readjustment of expression relations in the first generation is not confined to the parental characters, but may involve the recall to expression of primitive charac-

ters transmitted in latent form from remote ancestors. It is one of many indications that the changes of expression relations which have to be ascribed to adjustment are quite as great as those which Mendelism has sought to explain by the theory of "character units" and of their segregation in "pure germ cells."

Writers on Mendelism have sought to connect the idea of a separation of character units with the processes of subdivision by which the germ cells are formed. The fact that four germ cells are formed by subdividing one mother cell has led to the suggestion that a separation of antagonistic character units might occur when this subdivision takes place. Two of the germ cells might contain the "unit" representing one of the contrasted characters and two other germ cells the unit of the other character. This would give equal numbers of germ cells of the two kinds which the theory of Mendelism requires. Nevertheless it is possible for this equality to be reached in another more practical way. The numbers of germ cells tending to express the contrasted characters will be equal if equal numbers of the mother cells become adjusted in the two ways before subdivision into germ cells takes place. Thus all the germ cells from the same mother cell may be of the same kind instead of being of two kinds. This view is more practical because it does not require us to suppose that the mother cells divide into unequal parts in forming germ cells. In view of the frequency of the phenomena of reversion and recapitulation it is much easier to suppose that both of the contrasted characters are transmitted, though only one comes into expression, than to believe that there is any separate transmission of character units in different germ cells.

SIGNIFICANCE OF PRIMITIVE CHARACTERS IN BREEDING.

Breeders will appreciate the practical importance of the fact that such a character as the green fuzz of cotton is not necessarily permanent, even though it may be shown by all the members of the first generation of a hybrid. As soon as we know that such a character is likely to disappear we recognize the need of carrying our hybrids over to the second and third generations before undertaking to make final determinations of their merits.

Even among the cotton hybrids it has to be considered that other and more important characters may be affected by the same principles as the green fuzz. In the first generation all the hybrids between the Central American types of cotton and our improved Upland varieties produced shorter lint than either of the parents. If the short lint had been looked upon as a permanent character, such hybrids would have been rejected as of no value in comparison with the parent varieties. Nevertheless, a series of these hybrids is being retained in order to learn whether the short lint will not behave like

a primitive character and give place to long lint in later generations. Indeed, this seems already to be taking place. Though the short lint does not disappear as promptly as the green fuzz, the second and third generations of the hybrids are showing examples of much longer lint than appeared in the first generation.

SUMMARY.

In hybrids between the Kekchi cottons of Guatemala and varieties of the Sea-Island and Egyptian series the seeds commonly show green fuzz in the first generation. This character does not normally appear in either of the parental varieties, though it is probably an ancestral character of both of them.

The reappearance of the primitive character in the hybrids is to be associated with other facts of reversion and recapitulation, and serves to indicate that these groups of phenomena are very closely related.

The fact that the green fuzz largely disappears in the second generation of the hybrids indicates that the recall of this character to expression in the first generation marks a preliminary stage in the process of conjugation. The complete results of conjugation first become visible in the second generation, when the parental characters reappear in many combinations and gradations. By thus recognizing that the first and second generations of hybrids represent different stages of the process of conjugation it is possible to understand the appearance and disappearance of such characters as the green fuzz without resorting to the complicated theory of Mendelism.

The practical point is that such departures from the parental characters in the first generation of a hybrid may not remain to detract from the value of later generations. Hybrids in which these undesirable primitive characters come into expression must be grown for at least two generations before selection can be effectively applied. The characters shown by the first generation do not afford any practical indication regarding the characters of the later generations.

Approved:

JAMES WILSON,
Secretary of Agriculture.

WASHINGTON, D. C., *October 12, 1908.*

[Cir. 18]

O